

Epidemiological studies of *Puccinia digitariae* and *Phyllachora paspalicola* on grasses at Nylsvley Nature Reserve

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Accepted 15 June 1988

An epidemiological study of two fungal diseases, *Puccinia digitariae* Pole Evans (a rust) on *Digitaria eriantha* Steud. and tarspot (*Phyllachora paspalicola*) on *Panicum maximum* Jacq. was undertaken at Nylsvley. Both incidence (percentage leaves infected per tuft) and severity (percentage leaf area infected) were recorded throughout the growing seasons 1978/79 and 1979/80. Disease progress curves revealed a growth in both rust and tarspot throughout the seasons with the maximum incidence (*I*) of rust reaching 59% in both seasons. Severity indices (*S.I.*) of rust attained a maximum of 0,24 in March 1980 and 0,14 in December 1978. The highest *I* and *S.I.* of tarspot occurred in February 1979 (51% and 0,22 respectively). The relationships between *I* and *S.I.* were also determined. The rust on *D. eriantha* appeared to increase relatively more by *I* than *S.I.* in the 1978/79 season and early months of the 1979/80 season, but conversely in the later stages of disease development in 1980. Tarspot increased more by *I* relative to *S.I.* in 1978/79 but conversely in 1979/80. Comparisons between disease progress curves of the two diseases and between two seasons are also presented. The influence of selected macroclimatic parameters on disease development is discussed.

'n Epidemiologiese studie van twee swamsiektes, *Puccinia digitariae* Pole Evans ('n roes) op *Digitaria eriantha* Steud. en *Phyllachora paspalicola* op *Panicum maximum* Jacq. is op Nylsvley onderneem. Insidensie (persentasie geïnfekteerde blare per rol) en omvang (persentasie blaar-oppervlakte geïnfekteer) was deur die groeiseisoene van 1978/79 en 1979/80 gemonitor. Siekte-progressiekurwes het op 'n toename van beide patogene gedurende die seisoene gedui, met 'n maksimum insidensie (*I*) van roes van 59% in al twee seisoene. Omvang (*O*) van *P. digitariae* het 'n maksimum van 0,24 in Maart 1980 en 0,14 in Desember 1978 bereik. Die hoogste *I* en *O* van *P. paspalicola* het in Februarie 1979 voorgekom (51% en 0,22 onderskeidelik). Die verwantskap tussen *I* en *O* was ook bepaal. Roes op *D. eriantha* het meer toegeneem in *I* as *O* gedurende die 1978/79-seisoen en die vroeë maande van die 1979/80-seisoen, maar andersom is die later stadia van siekte-ontwikkeling in 1980. *P. paspalicola* het meer in *I* vergeleke met *O* in 1978/79 toegeneem, maar weer eens is die teenoorgestelde tendens in die 1979/80-seisoen ondervind. Vergelykings van siekte-progressiekurwes van die twee siektes van die twee seisoene word ook gegee. Die invloed van geselekteerde makroklimaat-parameters op siekte-ontwikkeling word bespreek.

Keywords: *Digitaria eriantha* Steud., *Panicum maximum* Jacq., *Phyllachora paspalicola*, plant pathogens, *Puccinia digitaria* Pole Evans

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Introduction

Plant disease exists in natural host populations but usually in the endemic state (Zadoks & Schein 1979), since natural ecosystems have evolved to produce a balanced interaction of component species. However, this does not necessarily mean that an endemic disease is never eruptive, showing a sigmoid increase. The development of such an epidemic is influenced not only by changes in host susceptibility or pathogen virulence, but also by environmental parameters. Despite the extensive knowledge of agrosystem diseases, little is understood about the role and importance of pathogens in the wild (Dinoor & Eshed 1984).

The herbaceous layer of the *Burkea africana* Hook. savanna at Nylsvley is comprised of several graminoid species, of which *Digitaria eriantha* Steud. and *Panicum maximum* Jacq. make up 27% and 1,7% respectively of the basal cover of 5,96% (van Rooyen & Theron 1977). A preliminary investigation revealed the presence of two foliar fungal parasites, *Puccinia digitariae* Pole Evans (Cummins 1971), a rust, and *Phyllachora paspalicola* (Parbery 1967), tarspot, on *D. eriantha* and *P. maximum*, respectively. Rusts are obligate biotrophic fungal parasites belonging to the Basidiomycetes and on *D. eriantha* are manifested as foliar lesions, or raised pustules which develop from localized yellow flecks (Figure 1). Tarspot is a member of the Ascomycetes and symptoms commence in the form of

foliar amber blisters which eventually mature as the clypei (fruiting bodies) (Figure 2).

The aim of this research was to ascertain the incidence and severity of these pathogens at Nylsvley, since few epidemiological studies on naturally occurring pathogens have been undertaken. This study was also a necessary prerequisite for further investigation of the impact, if any, of foliar grass disease on biomass. The methods employed were designed to achieve several aims: (1) The measurement of the incidence and severity of infection throughout the two seasons. (2) Comparisons of growth rates and patterns of the disease progress curves between the two seasons. (3) The relationship between incidence and severity (*S*) of disease, and (4) to attempt to explain the differences in disease progress between the two seasons based on relevant macroclimatic parameters.

Materials and Methods

Field methods

Samples were collected over two growing seasons (October 1978–March 1979 and October 1979–April 1980). Sampling was performed every 2 weeks. Preliminary rating experiments throughout the research area (50 ha) indicated that both rust and tarspot were evenly distributed between sites within the area (the difference between incidence and severity between sites was never greater than 2% at any given

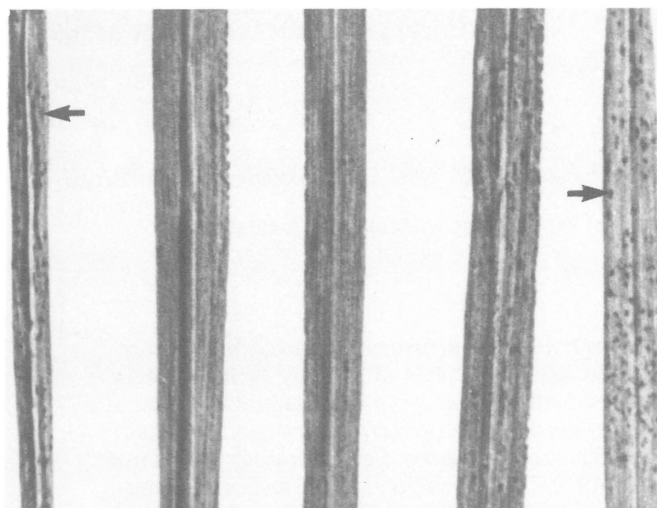


Figure 1 *Digitaria eriantha* leaves infected with *Puccinia digitariae*. Note pustules (arrows) on leaf surface.

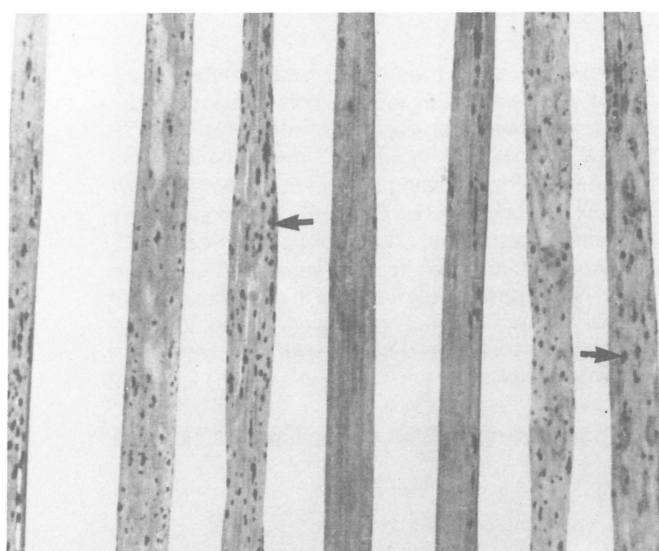


Figure 2 *Panicum maximum* infected with *Phyllachora paspalicola*. Note the clypei or tarspots (arrows) on the leaf blades.

time). Therefore six line transects (10 m long) were taken from 10 sites (each approximately 500 m²) within the research area (50 ha). Grass tufts falling on the transect line or 0,5 m on either side, were sampled. The number of tufts per line transect varied from 20–40 depending on the density of the species or specific site. The sample areas were deliberately chosen from areas densely populated with *D. eriantha* or *P. maximum*. The average distance between tufts also varied from 5–100 cm, but all tufts were sampled. Whole tufts were rated for incidence (*I*) and severity (*S*) of disease to overcome sampling bias as fungal spores often land on more accessible outer leaf blades. Only living leaf blades were sampled. The average *I* and *S* of disease was calculated for each tuft, then all the tufts on the transect followed by all the transects in the ten sampling sites at a given sampling time.

Incidence and severity

Disease incidence (*I*) plant⁻¹ was calculated as the percentage infected leaves per tuft. The average severity (*S*) plant⁻¹ was estimated as the percentage of leaf area affected by lesions. From these ratings, average *I* and *S* figures

were calculated for the six transects within each 500-m² area, followed by average figures for all ten sampling areas.

A key, based on James (1971), was devised to assess disease severity: leaves were categorized into several infection classes (0%, 1–5%, 5–10%, 10–25%, 25–50%, 50–75%, > 75%) based on the percentage leaf area infected. The severity index (*S.I.*) was calculated as follows:

$$S.I. = \frac{\text{sum of all disease ratings}}{\text{total no. of ratings} \times \text{max. disease grade}}$$

where the maximum disease grade (> 75%) was 6 on the 0–6 scale.

The average incidence and severity index values were then plotted on a time basis, thereby generating disease progress curves defining the course and pattern of the diseases. Rather than take the area under the disease progress curves (AUDPC) which tends to mask the distinction between true progressive and degenerative phases, it was decided to compare only the slopes of the progressive growth phases of the diseases. Where the curves were non-linear ($r < 0,95$), they were transformed into straight lines by linear regression (Table 1). The significances between two linear regressions were tested by comparing the two respective slopes.

The relationship between incidence and severity for each disease in each season was established to determine whether disease progress increased more by *I* relative to *S* or conversely. An exponential equation (James & Shih 1973) was used:

$$I = 100 (1 - r^S)$$

where *I* = incidence, *S* = severity, $r = e^{(1/b)}$, *b* = regression coefficient.

The equation satisfies the condition that *I* = 0 when *S* = 0, and that as *S* increases, *I* also increases until the incidence approaches 100%. A larger *r* value implies that disease increases relatively more by *S* than *I*, and conversely, a smaller *r* value means disease increases more by *I* than *S* (James & Shih 1973).

Macroclimatic data

Since it was not feasible to collate vast quantities of macroclimatic data with disease progress, and microclimatic data

Table 1 Linear regression analysis of the progressive phases of disease progress curves of *Puccinia digitariae* and *Phyllachora paspalicola*

1978/79 growing season		
<i>Digitaria</i> incidence		<i>Panicum</i> incidence
$r = 0,97$		$r = 0,77$
$a = 0,12$		$a = 0,12$
$b = 0,02$		$b = 0,01$
Severity		Severity
$r = 0,96$		$r = 0,87$
$a = 0,03$		$a = 0,02$
$b = 0,002$		$b = 0,002$
1979/80 growing season		
<i>Digitaria</i> incidence		<i>Panicum</i> incidence
$r = 0,80$		$r = 0,82$
$a = 0,41$		$a = 0,19$
$b = 0,001$		$b = 0,01$
Severity		Severity
$t_1-t_3: r = 0,89$	$t_4-t_7: r = 0,80$	$r = 0,95$
$a = 0,12$	$a = 0,04$	$a = 0,02$
$b = 0,002$	$b = 0,002$	$b = 0,004$

r = regression coefficient

b = slope

P = 0,05

a = y-axis intercept

was inconsistent, it was decided only to attempt to explain the differences in disease progress between the two seasons, based on two important parameters, water and temperature. These parameters were chosen in terms of their influence on fungal spore germination, dispersal and growth.

It has been widely demonstrated and accepted that many epidemiological effects are related to free water (which reaches the leaf surface by precipitation or condensation) and temperature (Rotem 1978; Zadoks & Schein 1979). The amount of water vapour can be expressed as relative humidity or saturation vapour pressure deficits. Saturation vapour pressure deficit may be more meaningful in biological systems as it is the difference between the saturation and actual vapour pressure for a given volume of air.

In particular, the effects of water and temperature on many Basidiomycetes, especially rusts (Mahindapala 1978) and Ascomycete spore behaviour have been established. Consequently, macroclimatic reports on total rainfall and number of rain days, relative humidity and saturation vapour pressure deficits, dew and temperature were

obtained from Dr Trevor Harrison at the Weather Report Station 2 at Nylsvley. These results are presented in Tables 2–4.

Results

P. digitariae on *D. eriantha*

The disease progress curves for *I* and *S* of rust on *D. eriantha* followed the typical pattern of a progressive growth phase, after which the disease reached a plateau and a degressive leg followed where leaf senescence took place and the pathogen slowed down until eventually the grass leaf blades died in winter. Only the progressive growth phases are compared in this study (Figures 3 & 4).

Linear regression analyses of the progressive growth phases are presented in Table 1. The regression coefficients were close to 1 for both incidence ($r = 0,97$) and severity

Table 4 Saturation vapour pressure deficits and dew data (from the synoptic charts at Nylsvley weather station 2)

Months	Saturation vapour pressure deficit (mb)			Dew	
	Av. monthly	Minimum	Maximum	Av. (mm)	No. of dew days
October 1978	13,4	1,8	4,3	0,05	3
November	11,4	8,8	9,3	0,09	11
December	13,6	—	—	0,08	12
January 1979	13,3	9,5	8,5	0,03	4
February	11,9	—	—	0,04	2
March	12,6	—	—	0,07	11
April	11,8	—	—	0,05	11
October 1979	14,7	3,8	12,45	0,00	1
November	10,3	2,3	—	0,02	3
December	11,7	—	—	0,02	4
January 1980	8,8	2,9	11,5	0,11	11
February	7,3	—	—	0,16	10
March	8,5	—	—	0,13	18
April	10,2	—	—	0,03	6

Table 2 Rainfall data from the main weather station at Nylsvley (1978–1980)

Year and month	Total rainfall (mm)	No. of rain days
August 1978	5,2	—
September	23	—
October	104,7	9
November	60,9	9
December	45,3	8
January 1979	36,2	8
February	56,1	7
March	18,9	9
April	19,0	4
August 1979	12,5	—
September	1,4	—
October	103,5	8
November	214,5	12
December	70,7	7
January 1980	152,5	18
February	98,2	15
March	38,0	7
April	42,6	4

Table 3 Average monthly climatic data from October 1978 to April 1980 (from the synoptic summary charts at Nylsvley weather station 2)

Months	Temperature (°C)			Relative humidity (%)		
	Av. monthly	Av. min.	Av. max.	Av. monthly	Max. morning	Max. afternoon
October 1978	21,5	24,5	27,8	47,4	88	99
November	22,0	18,0	21,3	56,4	84	67
December	23,2	—	—	51,9	—	—
January 1979	23,4	18,3	23,6	53,4	89	61
February	23,7	—	—	59,0	—	—
March	22,4	—	—	53,1	—	—
April	20,8	—	—	51,5	—	—
October 1979	22,7	16,1	22,1	46,1	93	70
November	21,6	17,2	23,0	59,6	95	85
December	22,5	—	—	56,8	—	—
January 1980	22,2	19,0	24,1	66,9	96	81
February	22,3	—	—	72,5	—	—
March	21,1	—	—	65,5	—	—
April	18,5	—	—	51,6	—	—

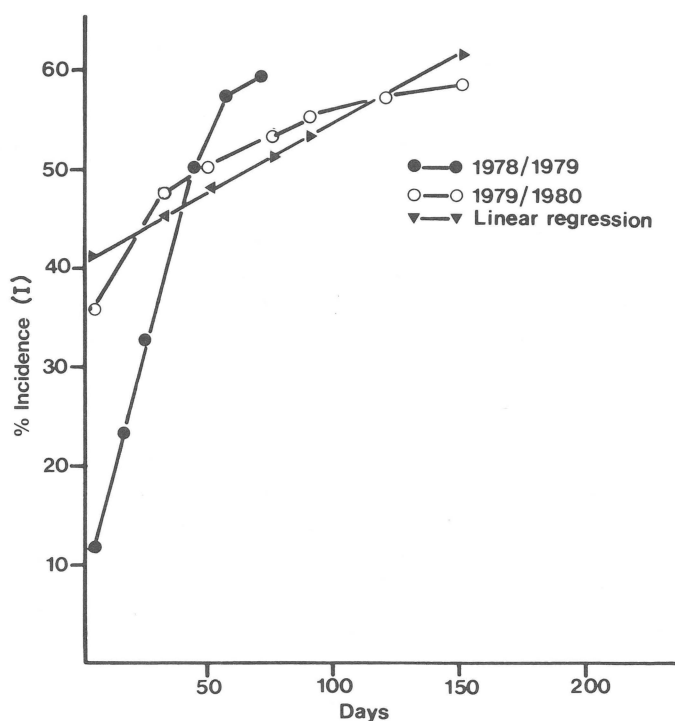


Figure 3 Incidence of rust on *D. eriantha* in the 1978/79 and 1979/80 season.

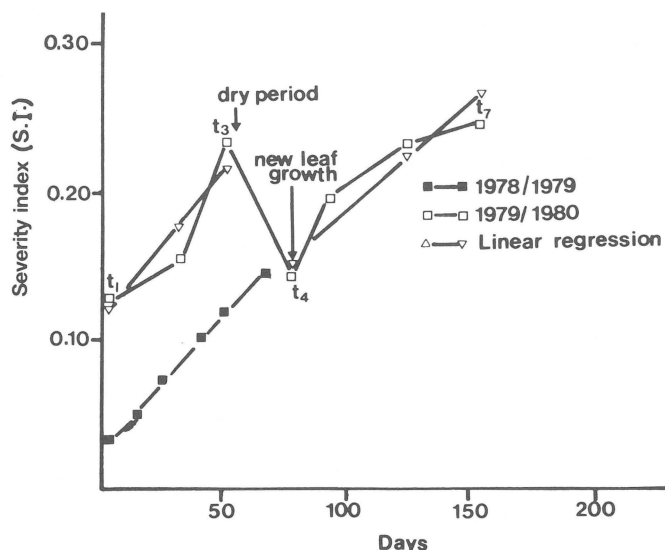


Figure 4 Severity index of rust on *D. eriantha* in the 1978/79 and 1979/80 season.

($r = 0,96$) for the 1978/79 growing season (October–March) and consequently only the untransformed curves are depicted for this season in Figures 3 and 4. Linear regressions are included for I and $S.I.$ for the 1979/80 growing season (October–April). The disease progress curves for I and S differed between the two growth seasons. The maximum I of rust was similar (58–59%) for both seasons but was reached earlier (December) in 1978 than in the following season where maximum I was attained in March 1980 (Figure 3). Maximum $S.I.$ was lower (0,14) in 1978 than in 1980, where the maximum $S.I.$ was 0,24 (Figure 4). The growth rate of rust in terms of I was greater in 1978/79 relative to 1979/80 (determined by comparing the linear regression slopes — Table 1; $P = 0,05$) whereas the growth rate of S of infection was similar in both seasons ($b = 0,002$) for both phases t_1 – t_3 and t_4 – t_7 (Figure 4).

The sudden decrease in S , observed in January 1980 followed by an increase (t_4 – t_7) was due to a dry period in December when many of the older grass leaves senesced and only live blades were assessed. There was a rapid new flush of leaves which were quickly colonized so I remained high but S dropped drastically for a short period, followed by a sharp increase.

The untransformed pattern of rust I in 1978/79 revealed a linear increase whereas in the 1979/80 growing season the I of infection followed a logarithmic pattern (Figure 3). S increase in 1978/79 was linear whereas S in 1979/80 for the initial periods t_1 – t_3 exhibited a slight exponential increase and in the latter period (t_4 – t_7) S increased logarithmically (Figure 4).

The relationship between incidence and severity (Figures 7 & 8) again illustrated that the rust infection on *D. eriantha* increased relatively more by I than S in the 1978/79 season (Figure 7, $r = 1,45$) and in the early months of 1979/80 [Figure 8 (t_1 – t_3), $r = 1,86$]. However this relationship behaved conversely in the later stages of the disease development [Figure 8 (t_4 – t_7), $r = 14,9$] in the 1979/80 season.

P. paspalicola on *P. maximum*

Linear regressions of I and S for the 1978/79 season and I for the 1979/80 season are presented in Table 1. The regression coefficient for S for 1979/80 was 0,95 and consequently only

the untransformed curve is depicted for $S.I.$ (Figure 6). In the first season the highest I and $S.I.$ of the disease occurred in February 1979 (51,4% and 0,22 respectively) whereas, owing to the later appearance of tarspot in the second season, maximum I and $S.I.$ (67% and 0,45 respectively) was observed in late March/early April (Figures 5 & 6). The growth rate of tarspot in terms of I was similar for both seasons ($b = 0,01$). However, the growth rate of the disease in terms of $S.I.$ was greater in 1979/80 ($b = 0,004$) than 1978/79 ($b = 0,002$).

The untransformed curves of tarspot revealed a logarithmic development for I in 1978/79 and 1979/80 (Figure 5). The growth of the disease in terms of $S.I.$ was linear in the first season but logarithmic in the second season (Figure 6).

The relationship between I and $S.I.$ can be observed in Figure 9 and 10. The smaller r value ($r = 1,28$) obtained in 1978/79 compared to 1979/80 ($r = 2,5$) indicated that the

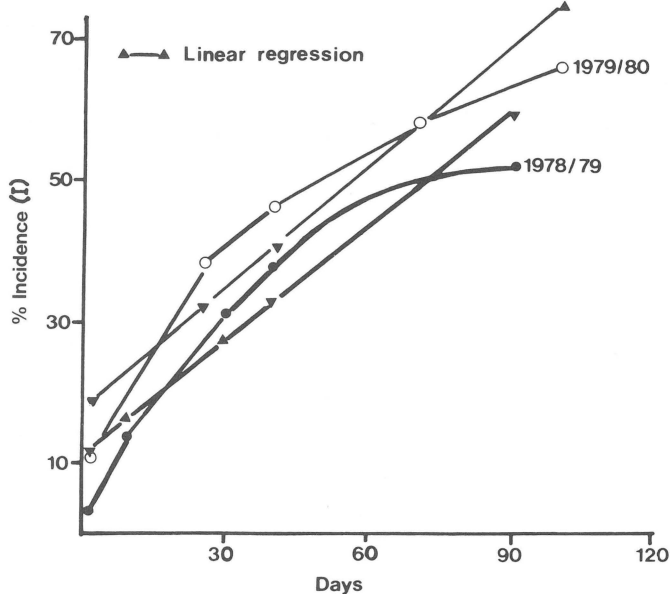


Figure 5 Incidence of tarspot on *P. maximum* in the 1978/79 and 1979/80 season.

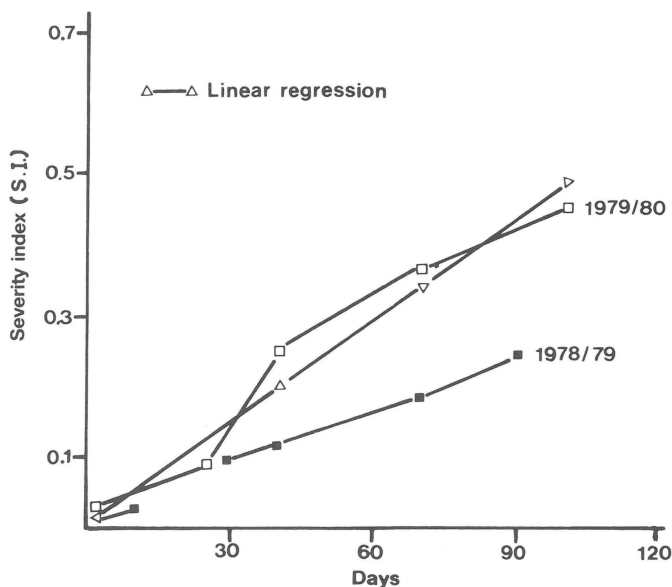


Figure 6 Severity index of tarspot on *P. maximum* in the 1978/79 and 1979/80 season.

disease increased more by *I* relative to *S* in 1978/79 (Figure 9) but more by *S* than *I* in 1979/80 (Figure 10).

P. digitariae and *P. paspalicola*

The relative growth rates of rust and tarspot can be assessed by comparing slope (*b*) values (Table 1). In the 1978/79 season the growth rate of *I* of rust ($b = 0,02$) was greater than tarspot ($b = 0,01$) whereas *S.I.* ($b = 0,002$) were similar for both diseases. In the following season tarspot exhibited a greater growth rate than rust with respect to *I* ($b = 0,01$ and $b = 0,001$ for tarspot and rust, respectively) and to a lesser degree with respect to *S.I.* ($b = 0,004$ and $b = 0,002$ for tarspot and rust, respectively).

Macroclimatic data

Macroclimatic data are presented in Tables 2–4. Temperature conditions were ideal (18–23°C) for rust and tarspot germination for the entire 1978/79 and 1979/80 seasons (Table 3). Rainfall was greater in September 1978 (23 mm)

than in 1979 (1,4 mm) (Table 2) which may explain the earlier appearance of rust in 1978 than 1979.

Late rainfall in January/February 1980, following a dry period in December 1979, influenced the pattern of rust development (Figure 4). Maximum humidity figures (Table 3) were favourable for spore germination in both October 1978 and 1979. However, the average number of dew days was higher in the early months (November and December) of the 1978 season compared to 1979, whereas the number of dew days in the later months (January–March) of the 1979 season was greater than 1978. *I* and *S* of tarspot were higher in January–March 1980 than the previous year (Figures 5 & 6).

Discussion

The study of the epidemiology of these two fungal diseases, rust and tarspot, indicated several interesting patterns. The

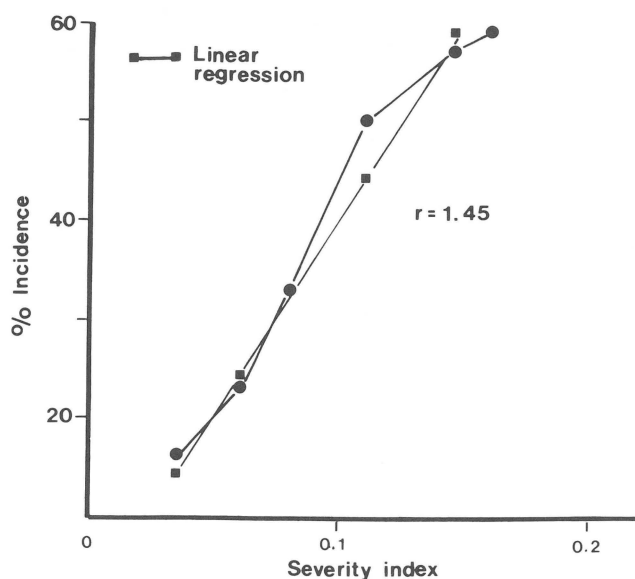


Figure 7 Relationship between incidence and severity of rust-infected *D. eriantha* in the 1978/79 season. $r = e^{(1/b)}$.

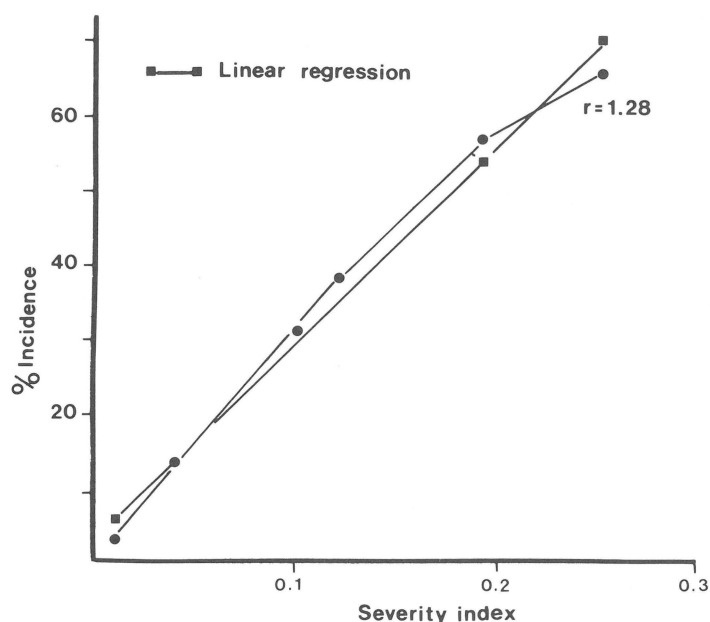


Figure 9 Relationship between incidence and severity of tarspot-infected *P. maximum* in the 1978/79 season. $r = e^{(1/b)}$.

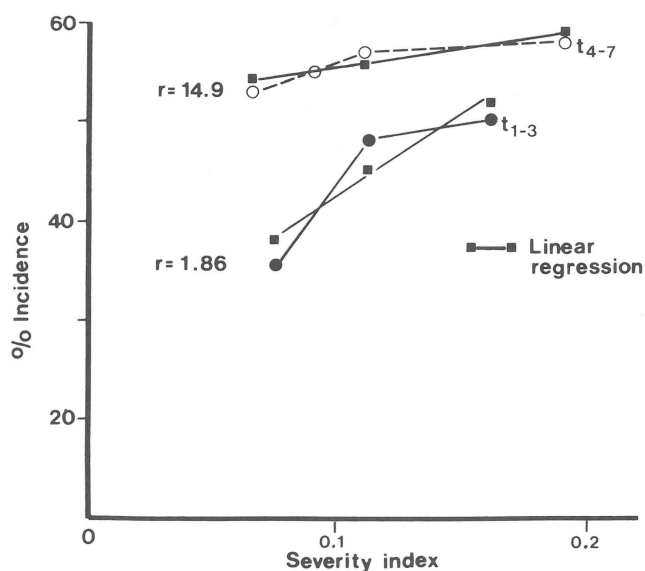


Figure 8 Relationship between incidence and severity of rust-infected *D. eriantha* in the 1979/80 season. $r = e^{(1/b)}$.

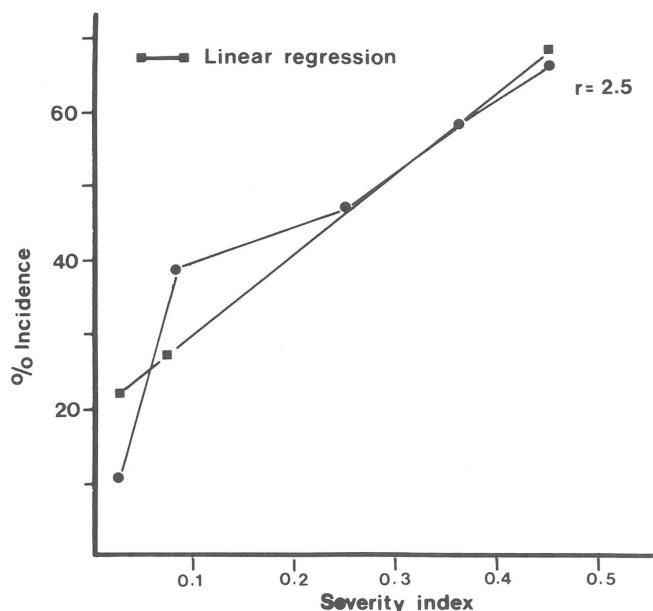


Figure 10 Relationship between incidence and severity of tarspot-infected *P. maximum* in the 1979/80 season. $r = e^{(1/b)}$.

linear nature of the disease progress curves in the progressive phases for rust on *D. eriantha* in the 1978/79 season (Table 1, Figures 3 & 4) indicated that the growth of this disease was not limited by tissue availability. The incidence and severity of the rust infection increased as the pathogen produced spores which landed on both infected and previously uninfected plants with both auto- and allo-infection. However in the case of rust on *D. eriantha* in the 1979/80 season the untransformed progress curve for incidence followed a logarithmic pattern (Figure 3) flattening off in mid-December following a dry period when many of the older grass leaves senesced, thus limiting the amount of live leaf tissue available. A second flush of leaves followed which were rapidly colonized and severity of infection increased (t_4 – t_7 , Figure 4) but then tailed off as the leaves began to senesce at the end of the growth season. Tarspot on *P. maximum* followed a similar slight logarithmic growth pattern in terms of incidence for both seasons (Figure 5). However, severity of infection was linear in its growth in 1978/79 and logarithmic in 1979/80 (Figure 6). Since there was a dry period in 1979 and the disease appeared later in this season than the previous year, it would seem that leaf tissue availability could have been a limiting factor in the 1979/80 season. Incidence of both rust (59%) and tarspot (67%) was always higher than severity throughout the seasons. This has been shown to be the case in most diseases where S is less and at most equal to I (Seem 1984). Since the resistance/susceptibility of these pathogens have not been extensively studied, one can only postulate that lower severity indices (S never succeeded 0,25 for rust and 0,45 for tarspot) may be attributed to some level of resistance within a non-agricultural environment. It has been suggested by several workers (Harlan 1976; Burdon & Shattock 1980) that pathogens of natural ecosystem plants may be partial or indirect controllers of species density and distribution. However, the tolerance of host plants to disease within an interactive ecosystem is difficult to assess or even quantify.

Studies of the relationship between incidence and severity are limited and only reflect the rate of increase of I relative to S in terms of allo- or auto-infection. For rust and tarspot, in 1978/79, there appeared to be a fairly uniform increase of severity with incidence (Figure 7 & 9). The smaller r values ($r = 1,45$ and $r = 1,28$ for rust and tarspot, respectively), reflecting that both diseases increased more by I relative to S , suggests that infection spread more by spores landing on nearby leaf blades than on the same leaf. On the other hand the rust infection on *D. eriantha* in 1979/80 (Figure 8) exhibited a large r value ($r = 14,9$) for the second period (t_4 – t_7) of growth. This pattern may be explained by the secondary leaf flush which was accompanied by high rainfall (152,5 mm), high relative humidity (96%) of the air in the grass canopy in the mornings (Table 3) and suitable spore germination temperatures (19–24,1°C; Table 3). Subsequent re-infection was rapid and the rust appeared to spread more by increased S than I . Tarspot on *P. maximum* in the 1979/80 season increased more by S relative to I . The first flush of leaves appeared late (in December 1979) and consequently the appearance of tarspot was later than in 1978. Rapid leaf growth was sustained by high rainfall from January to April (Table 2). *P. maximum* leaves were in a more advanced stage of development from January 1980 onwards, and these mature leaves appeared

to be more susceptible to infection than the declining number of immature leaves available for colonization. Thus susceptibility to tarspot appears to increase with leaf age and time of year. Jones & Hayes (1971) have also shown that in oats, infected with *Erysiphe graminis*, susceptibility usually increases with leaf age.

Rainfall, in its inevitable relationship with free moisture essential for both pathogen spore germination and plant growth, and temperature are critical environmental factors affecting the development of fungi on the grasses *D. eriantha* and *P. maximum*. The temperature range for most fungal spore development is 18–25°C and relative humidities between 95 and 100% are usually required for germination (Mahindapala 1978; Rotem 1978). Indeed, this temperature range (Table 3) was present at Nylsvley for both growing seasons. The earlier appearance of rust in 1978 than in 1979 may be partially explained as a consequence of more rainfall in September 1978 (23 mm) compared to 1979 (1,4 mm). These early rains in 1978 were followed by favourable humidity (maximum 99%), and saturation vapour pressure deficit (13,4) conditions (Tables 3 & 4) in October 1978. In the case of both rust and tarspot, rainfall and number of dew days had a significant influence on the pattern of disease development in the latter months of 1979/1980. Late rains (Table 2) and high number of dew days (Table 4) in 1980, compared to 1979, resulted in not only a new leaf flush of *D. eriantha* but reduced leaf senescence of both grasses, accounting for continued disease growth until late April and therefore higher final I and S . Unfortunately microclimatic and other macroclimatic data were inconsistent and therefore could not be used for comparative studies. Consistent and reliable microclimatic data may in future prove useful.

From these studies, the stage of leaf growth, time of infection, tissue availability and rainfall seem to be important in disease progress. The incidence and severity of rust and tarspot would appear higher than expected in a natural environment, especially tarspot on *P. maximum* (Figures 5 & 6). It is speculated that the balances of co-existing host and pathogen populations have been disturbed by intensive grazing pressure and defoliation as a result of cattle and increased herbivore populations which were introduced into Nylsvley 20–30 years ago. Grazing pressure has been shown in some cases to reduce vigour of grass species (Roberts *et al.* 1975) and increase disease. Indeed *P. maximum* and *D. eriantha*, in particular, are extremely palatable and heavily grazed (Owen-Smith 1982).

This study, of the epidemiology of fungi on two grasses at Nylsvley, indicated the direct impact that pathogens can have on single populations in a natural ecosystem. It does not, however, address the problems of disease in a heterogeneous population or what overall effect plant disease can have within a dynamic equilibrium of plant communities. Pathogens in low numbers may be regarded, in terms of their potential role as a positive selection pressure on population dynamics and biomass or energy recycling, as 'co-existors'. Many questions still remain as to the role of pathogens in a natural ecosystem but much more integrated research in terms of population studies is required to provide further answers.

Acknowledgements

We thank the CSIR for their financial support and Professor V.H. Whitlock for translating the abstract into Afrikaans.

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